

DISPERSAL FOR SURVIVAL: SOME OBSERVATIONS ON THE TRUNK ANT (*FORMICA TRUNCORUM* FABRICIUS)

by

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ABSTRACT

The survival chance of the trunk ant (*Formica truncorum*) is compared with the survival chance of two other species of red wood ants: *F. rufa* and *F. polycтена*. Nest populations of *F. truncorum* are much smaller than nest populations of the other red wood ant species, which makes the species a weaker competitor. Moreover, *F. truncorum* has to move more often, as its nests are small and untidily built, which makes the species more dependent on external heat for raising its brood. In order to survive, the greater extinction chance of *F. truncorum* should be compensated by a greater colonization chance. The colonization chance depends on the number of queens produced, their chance of becoming fertilized and their chance of becoming adopted by *F. fusca*. It appeared that nest populations of *F. truncorum* produced less sexuals than those of the other red wood ant species, while there are no good arguments to assume that their queens will have a greater chance of becoming fertilized or that the queens are more skillful in finding a suitable nesting place. It is argued that local populations of the trunk ant are more prone to extinction than those of *F. polycтена* and *F. rufa*, at least in the sandy areas of west and central Europe, where most *F. truncorum* colonies are monodomous and largely also monogynous. So *F. truncorum* queens should have a greater chance to become adopted by *F. fusca* than *F. rufa* and *F. polycтена*. Adoption experiments can solve this problem.

KEY WORDS: Formicidae, red wood ants, *Formica truncorum*, survival, dispersal.

INTRODUCTION

The extinction chance of a species depends upon the size of its distribution area and the degree in which (meta)populations are isolated. A metapopulation of an ant species can be defined as a cluster of local populations between which exchange of genes is possible by means of flying sexuals. The (regional) survival chance of such a metapopulation depends upon the ratio between the extinction rate of local populations and the colonization rate of unoccupied habitat patches. If the extinction rate exceeds the colonization rate over a long period of time, then the metapopulation will become extinct in the end. In the case of red wood ants (*Formica s.str.* species), a local population may be one nest population (monodomous

colony) or a cluster of nest populations which can exchange their workers (polydomous colony). Red wood ant species differ in their tolerance to accept young queens in their nest: nestpopulations of some species have many queens (polygynous nests), while others have normally just one queen (monogynous nests). Nest populations that possess many queens can split off daughter nests, which results in a polydomous colony. Polygyny will have consequences for the survival chance of a species as it may lower the risk of regional extinction. Polygynous colonies can survive for many decades (up to one hundred years). So the extinction rate of local populations may be very low. However, the colonization rate of vacant habitat patches may also be low, as for establishing a colony a queen has to penetrate a nest of a *Serviformica* species and this is a very risky enterprise (GÖSSWALD, 1952, 1989). The low colonization chance makes red wood ant species vulnerable: they are decreasing in some parts of Europe and are mentioned in the IUCN Red List of Threatened Animals (1996). However, the trunk ant (*F. truncorum*) is not mentioned. This omission seems to imply that the trunk ant, which normally possesses one or a few queens, is less vulnerable than the other red wood ant species. In order to examine the vulnerability of *F. truncorum*, its survival chance will be compared to two other red wood ant species: *F. rufa*, which colonies may possess one queen or up to a few hundred queens and *F. polychteta*, which polydomous colonies possess many queens, up to a few thousand (GÖSSWALD, 1989). To estimate the regional survival chance of *F. truncorum*, the extinction chance of nestpopulation should be examined, as well as the colonization chance of the species. In order to get an impression of the population dynamics of *F. truncorum*, its distribution area in The Netherlands was surveyed during seven successive years (1989-1995). In summer (June-August) nests were counted and mapped to registrate changes in the number and the distribution of the nests. Some observations on dispersal (wedding flights) were made to see if flying queens are able to orientate on the landscape to increase their colonization chance.

DISTRIBUTION AND HABITAT

The distribution area of *F. truncorum* covers a large part of northern and central Europe and extends into Siberia (fig. 1). The species is quite common in northern Europe, but it is lacking in large parts of its distribution area in central Europe. Here it occurs mainly in mountainous areas. *F. truncorum* occurs only sporadically in the European lowlands. So the species has more or less a boreoalpine distribution (BETREM, 1960). It prefers xerothermic habitats. In the Netherlands the species is only

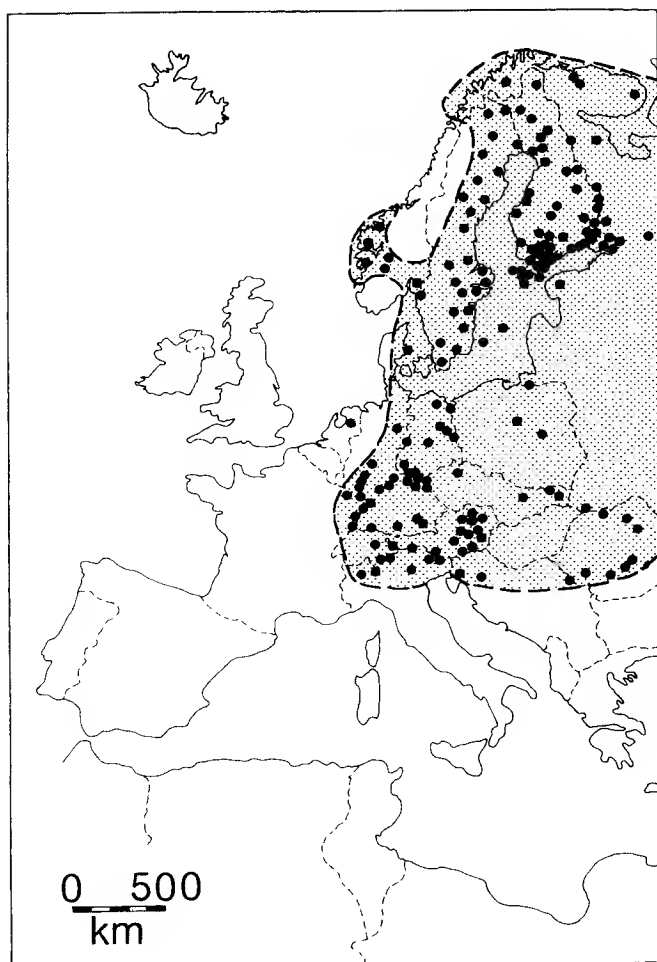


Fig. 1. Distribution of the trunk ant (*Formica truncorum*) over central and western Europe, showing the isolated position in the Netherlands.

found within a very limited area of 290 km². Within this area potential habitat was mapped on the basis of vegetation: open oak–birch and pine forest, southern exposed forest edges and open heath–grassland near trees or bushes, all on dry, sandy soil. In total 118 habitat patches were mapped, of which 25 were occupied. Most of these patches were rather small: about one third of the occupied patches are smaller than 1 ha. In total 256 ha was available for *F. truncorum* (0.9% of the distribution area). Much more habitat is available on dry sandy soils in the eastern part

of the country, but the distance to these areas seems to be too great to colonize it. Nests were found in open areas, open woodland and on the southern edge of dense woodland. About 100 *F. truncorum* colonies were found. Most nests of these colonies (ca. 70%) are built against the southern side of a tree trunk or a fallen tree, while the others are built against the southern side of a tussock of grass or heather. Nearly all nests are situated within a distance of 10 m from the nearest stable food source: a tree or bush with aphids, which are milked by the ants. In addition to this carbohydrate-rich aphidmilk, the ants need protein-rich food from insects. As carrying prey is more successful in open field, trunk ants avoid dense vegetations of Blueberry (*Vaccinium myrtillus*) and grasses (mainly *Deschampsia flexuosa*). Nests are preferably built on patches that are bare or sparsely overgrown by heather (*Calluna vulgaris*) and grasses. The Besthmenerberg near Ommen is considered as the core area, as it has the largest local population (ca. 30 nests) and the highest nest density (ca. 10 nests/ha).

EXTINCTION CHANCE

The extinction chance of a local population depends upon the number of nest populations which can support each other by mutual contact via worker ants. If a nest population loses its queen(s), workers of a neighbouring population can supply the nest with a new one. The extinction chance of a nest population depends on its 1) number of queens, 2) population size and 3) the quality of its habitat (availability of suitable nesting sites and food). We will discuss these factors in order to get an impression of the extinction chance of the core population in our study area.

Queen number and population size

WASMANN (1909), LANGE (1958) and BETREM (1960) found exclusively single nests and concluded that *F. truncorum* is a monogynous species, but later polydomous colonies were found in Switzerland (KUTTER, 1964), Germany (PREUSS, 1979) and Finland (SUNDSTRÖM, 1989, 1993; ROSENGREN *et al.*, 1985, 1986, 1993). In Finland, where the species occurs quite commonly on islands near the coast, nesthills were often connected with each other by means of nesting material which was spread between stone crevices (fig. 2). The number of queens and workers of eight colonies were counted by excavating the nests (ROSENGREN *et al.*, 1985). The number of queens varied between 1 and 15 per nest

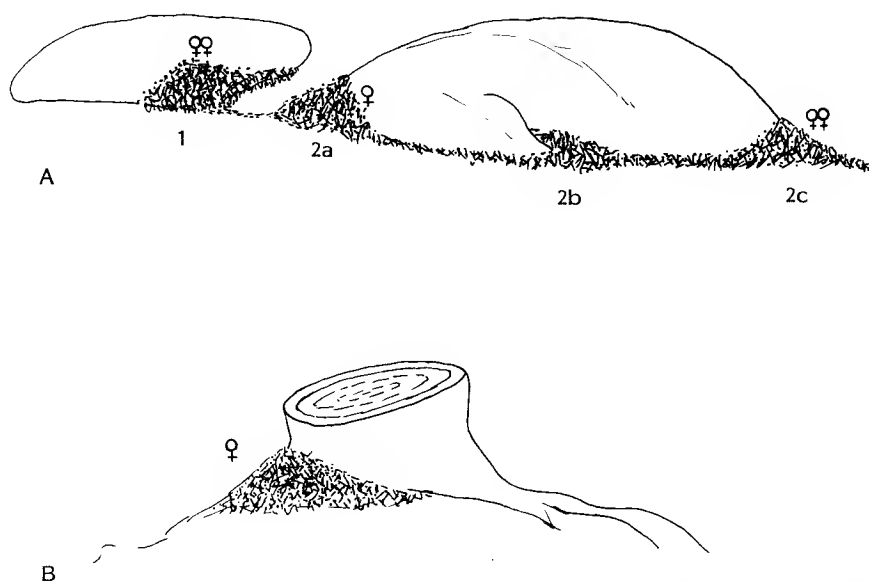


Fig. 2. Nests of *F. truncorum*. A. Nests under and around large stones; the polydomous colony consists of two nests, both containing queens (Finland); B. nest against a tree trunk, containing one queen (The Netherlands).

(ca. 6 queens on average). A large number of the colonies sampled by SUNDSTRÖM (1993) in a similar area contained even more than 20 wingless queens. Most of them were inseminated and laid eggs. Accepting more queens in a nest will make the nest population less vulnerable, as if one queen dies, her egg-laying task may be taken over by the other queens. So, polygyny will reduce the extinction chance of a nest population (ROSENGREN & PAMILO, 1983).

Most nests in our study area are single: on average 85% (82-95% yearly) over a period of seven years. Occasionally one or more daughter nests were built within a few metres from the mother nest. During such a nest splitting process several (unwinged) queens were transported to the new nest site. Often mother and daughter nest(s) produced offspring the following year, indicating that both nests had at least one queen. So the polydomous colonies were polygynous. As long as the nests that belong to such a colony have a common foraging area, workers will be exchanged. After some time the nest populations may fuse to one monodomous colony or they can move to another nesting site. When they stop sharing their foraging area, they become two monodomous colonies. So the number of nests belonging to a colony may change in time. Table 1 illustrates this for part of one local population. Most nests (61%) stayed

TABLE 1

F. truncorum colonies from part of the core area (Besthenerberg, Ommen) in the period 1989-1995; 1 = monodominant colony, 2 = polydominant colony (2 nests), 3 = polydominant colony (3 nests), → = moving of nestpopulation.

year/hr	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	Tot.
89	1	2	1	1	1	2	1	1	1	1	2	0	0	1	1	2	1	1	0	2	1	1	2	1	0	1	22
90	2	1	1	1	1	1	1	1	0	1	1	0	0	4	2	4	→1	1	0	1	2	0	1	1	1	0	20
91	1	1	0	1	1	1	1	→1	0	1	1	0	0	2	1	1	1	1	0	1	2	0	1	1	1	0	19
92	1	1	0	1	→1	1	1	0	0	1	1	1	0	1	1	1	1	→1	0	1	1	0	1	1	1	0	19
93	→1	1	0	1	2	0	→1	0	0	1	→3	1	0	→2	→1	→1	1	1	0	1	2	0	1	0	→1	0	17
94	2	1	0	1	2	0	1	0	0	1	2	1	1	2	1	2	1	2	1	1	2	0	1	0	2	0	19
95	2	1	0	→1	1	0	0	0	0	0	1	2	2	2	1	2	→1	1	1	1	→3	0	2	0	2	0	17

monodomous during the observation period of seven year, which suggests that they contain one or a few queens. The more queens there are in a nest, the more offspring can be produced. The average number of eggs laid per queen in a polygynous colony will be less than in a monogynous one, as a result of competition between the queens (WILSON, 1974; HERBERS, 1993; HEINZE, 1993), but on the other hand more queens can produce eggs during a longer life span of the colony (MABELIS, 1986). The number of workers of the Finnish colonies were estimated at ca. 3,000 for a small nest, at ca. 10,000 for a middle sized nest and at ca. 70,000 for a very big nest (ROSENGREN *et al.*, 1985). The nests that we found in the Netherlands and Poland belong to the category small and middle-sized. Such small populations have a small foraging area in comparison to the other red wood ant species (i.c. 55-750 m², 213 m² on average). Consequently they will have a relatively great extinction chance.

Nesting sites

F. truncorum nests are rather untidily built: pine needles and small twigs are accumulated irregularly against the southern side of a tree trunk, a laying tree stem, a heather bush or a grass tussock. The nests are rather small, which implies that less heat can be produced in the nest (STEINER, 1924; BRANDT, 1980a). Moreover, their structure is different from the bell-shaped mounds of *F. rufa* and *F. polycтена*. The regulatory system to produce (COENEN STASS *et al.*, 1980; KNEITZ, 1964) or dissipate heat by enlarging nest openings, works less well in the case of *F. truncorum* (ROSENGREN *et al.*, 1985). The inability to maintain thermal homeostasis results in a greater dependency on external heat for raising brood (KATÔ, 1939; ROSENGREN *et al.*, 1985) and the species is more thermophilic than *F. rufa* and *F. polycтена*. As a proper moisture gradient is essential for regulating the nest temperature (HORSTMANN & SCHMID, 1986), the workers prefer to build their nests against objects that can keep moisture and heat for a long time, such as tree trunks and tree roots. After a few heavy storms in 1972 and 1973 many trees fell down and many nesting places came available, especially on the Besthmenerberg, which is now the core area for *F. truncorum*. However, trunks and tree stems will decay gradually and the nestpopulation will have to move after some time to a more suitable nest site. If no suitable trunks, roots or stems are available within walking distance of the ants from the nest (max. 25 m), the population has to find something else to support the nest, e.g. a tussock of grass or heather. Within a period of seven years relatively more nestpopulations made use of grass tussocks for supporting their nest. In the core area the number of colonies that exclusively used tussocks increased from 11 (out of 43 colonies = 26%) to 15 (out of

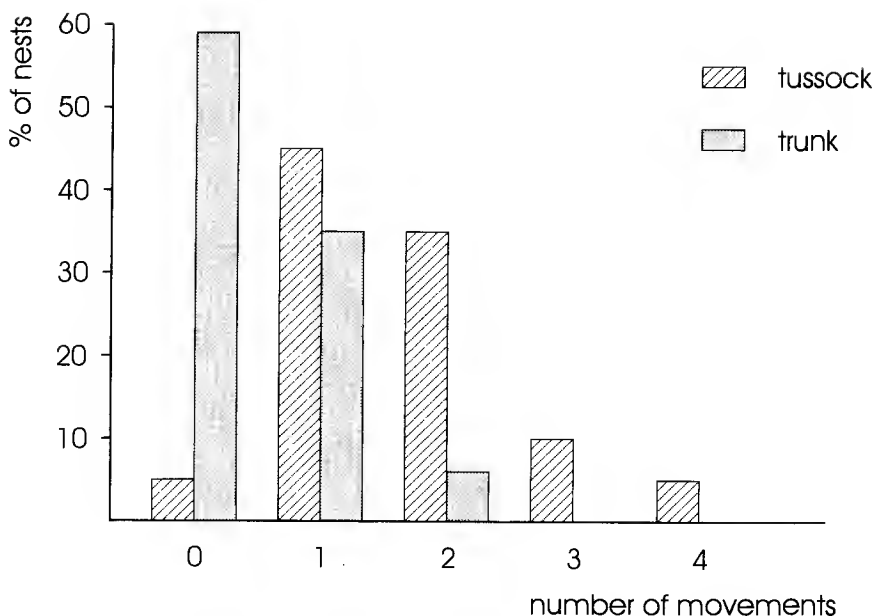


Fig. 3. Percentage nest populations that moved within a 7 year period. Grey bars: nests built against a tree trunk ($n = 34$), hatched bars: nests built against a grass tussock ($n = 20$); nearly 60% of the populations that built their nest against a tree trunk did not move at all. From polydomous colonies only the main trunk nest is taken into account. Nestpopulations that moved from a trunk to a tussock (or vice versa) within the 7 year period are omitted.

34 colonies = 44%), while the number of colonies that used trunks during that period dropped from 32 (out of 43 = 74%) to 19 (out of 34 = 56%). Grass tussocks deteriorate more quickly than tree trunks. Consequently, populations that built their nest against a grass tussock moved more often than populations that built their nest against a tree trunk (χ^2 test: $p < 0.005$; fig. 3). The occurrence of removals implies that the discovery of an abandoned nest should not lead to the conclusion that the nestpopulation became extinct, as it can be due to the removal of the nestpopulation to another nest site. In such cases the environment of the abandoned nest was thoroughly surveyed for new nest sites.

As moving is risky with regard to predators, like other ant species and birds, a nest population has a greater chance of becoming extinct if it has to move more often. Within a period of seven years no significant difference was found between the extinction rate of tussock nests and trunk nests, but it seems likely that the decreasing density of suitable tree trunks will affect the extinction and colonization chance of *F. truncorum*.

Competition

Ant populations are more likely to compete the more their habitat requirements overlap. So competition between nest populations that belong to the same species may be strongest. However, nest populations that belong to a polydomous colony exchange workers and food regularly and do not compete at all (ROSENGREN *et al.*, 1985). Workers from monodomous colonies seem to avoid each other. Aggressive encounters are rarely observed, even in situations where the distance between the colonies is small (fig. 4). After luring workers from two colonies, that are situated 13 m apart to the same bait, we observed only some biting and pulling on legs and antennae, but no serious fights. A similar result was obtained when workers of two monodomous colonies, which were situated 30 m apart, were lured to the same bait. Aggression between workers of different nests may increase with distance between the nests, as was observed by ROSENGREN *et al.* (1985), but according to these authors this is more probabilistic than deterministic. Once we observed that young workers and pupae from a *F. truncorum* nest were transported by conspecifics to another monodomous colony, over a distance of 30 m. This can be interpreted as robbery or as fusion of two nest populations. The result is that one of the two colonies became "extinct".

From the group of red wood ant species that occur in the area, *F. pratensis* is a greater potential competitor of *F. truncorum* than *F. rufa* or *F. polystena*, because it builds its nest in similar open habitats. Moreover, the food requirements of these species are quite similar, as they milk the same aphid species and both are generalists with respect to prey. However, the species may compete only locally, as the density of *F. pratensis* is very low: 2 colonies per 100 ha habitat. It is likely that *F. truncorum* will compete more often with *F. sanguinea* in the study area. Both species live in similar open habitats and they use not only similar food items, but also similar nest sites. The distribution pattern of the species in parts of the study area where nest densities of both species are high, indicates competitive exclusion (fig. 5). However, aggressive encounters between the species were rarely observed, not even in situations in which the distance between the nests was very small: a few metres and in one situation even one metre. Only occasionally a dead worker was brought to the nest of the opponent. We could not provoke a serious conflict by luring workers of the two species to the same bait (fig. 4). Most often they avoided each other and we have only indirect evidence of competitive exclusion, namely that several nests of *F. truncorum* were taken over by *F. sanguinea*. The latter species seems to be more skillful in winning a contest. ROSENGREN *et al.* (1986) observed raids of *F. sanguinea* on *F. truncorum* nests, which were introduced in their foraging area.

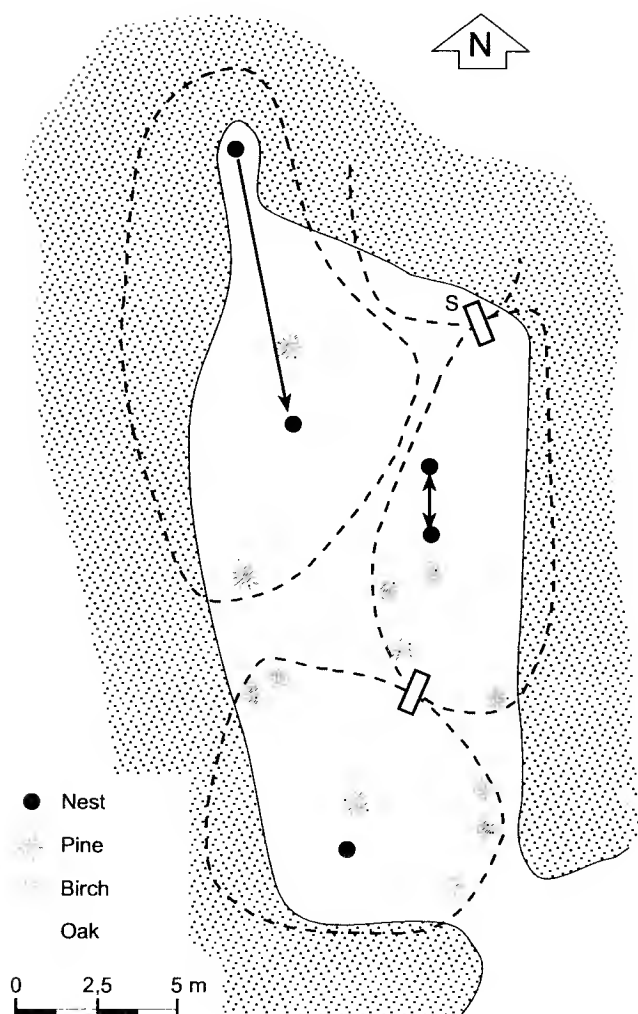


Fig. 4. Territories of three colonies of *F. truncorum* in an open area within a young forest plantation (grey), arrow = transport of workers and brood (from a trunk to a grass tussock and between two grass tussocks), s = nest of *F. sanguinea*, rectangle = feeding place, dashed line = border of foraging area, the most important food sources (trees with aphids) are indicated.

The overlap in habitat requirements between *F. truncorum* and *Coptoformica* species (*F. exsecta* and *F. pressilabris*) is less; *Coptoformica* species build their nests in dense grass vegetations, which are avoided by *F. truncorum*. In situations where the distance between nests of the two

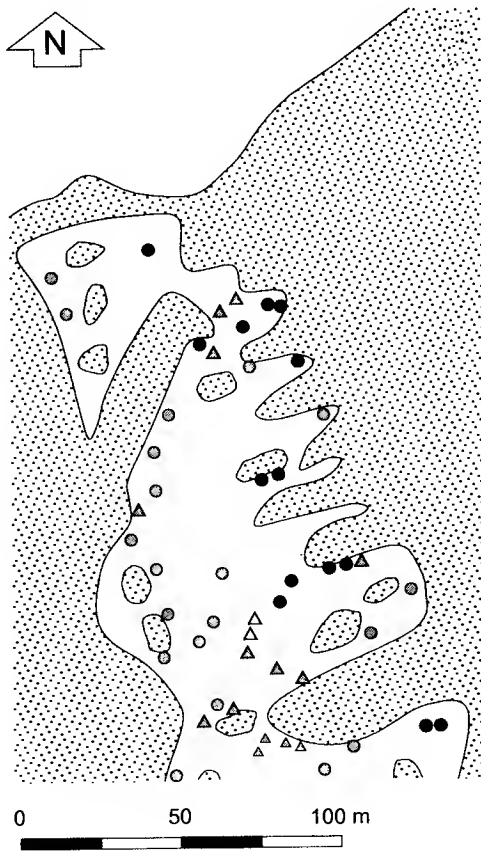


Fig. 5. Distribution of ant nests in an open area, surrounded by woodland (grey); black circle = nest of *F. truncorum* (14 nests = 9 colonies), grey circle = nest of *F. sanguinea* (20 nests), grey triangle = nest of *F. exsecta* (12 nests), white triangle = nest of *F. pressilabris* (3 nests). Five *F. sanguinea* nests in the eastern part of the open area belonged formerly to *F. truncorum* (situation: August 1995).

species is small (e.g., 8 m) they can maintain their position for years. In conclusion: a nest population has a greater extinction chance if the nest is surrounded by aggressive competitors, like *F. sanguinea*. This situation occurs in parts of our study area.

Succession of the vegetation

F. truncorum builds its nest on sunny sites near some trees or bushes. However, as trees grow higher, parts of these sites will get too much shade (fig. 6). The nest population will not get enough solar heat for a

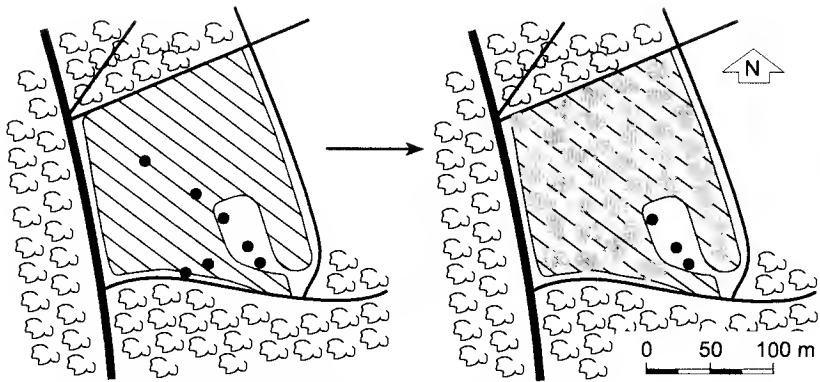


Fig. 6. Extinction of four nestpopulations seven years after planting young pine trees in a ploughed area (hatched) surrounded by forest (see fig. 4).

proper development of the brood in the nest: it has to move to a better site or it will become extinct. In a young pine plantation (2.5 ha), four nest populations became extinct during a period of seven years as a result of tree growth; the other three nest populations still got sun and survived (fig. 7).

COLONIZATION CHANCE

No local population is large enough to ensure long-term survival. For long-term survival colonization of suitable habitat patches is necessary to compensate for losses of local populations. The colonization chance of a habitat patch depends upon the number of queens produced by nearest nests, the chance of these queens to become fertilized, their capacity for orientation and dispersal and their chance to become adopted by a host species. These factors will be discussed in the next paragraphs.

Production of sexuals

Sexuals (males and females) are produced from mid July till mid August. During this period the presence of sexual pupae in the nests was checked nearly daily by lifting a thin board which was situated on the southern slope of the nests. In the early morning the ants brought their pupae under the board, *i.e.* the warmest place in the nest during that period. The number of nests that produce sexuals varied between 70 and 85% per year (over a period of 4 years). Males are produced earlier than females, although there is overlap in many nests. Sexuals left the nest flying within a period



Fig. 7. Part of the core area Besthmenerberg near Ommen showing small open areas within a forest, which are suitable as habitat of *F. truncorum*; the ants will move as soon as the nest site becomes too shady.

of one hour in the morning (between 8 and 11; fig. 8). The total number of males and queens that left the nest on several successive days was very small in comparison to other red wood ant species: generally not more than a few hundred. On the other hand more *F. truncorum* nests produced sexuals yearly than *F. rufa* and *F. polystena* nests: ca. 80% ($n = 30$), 68% ($n = 22$) and 47% ($n = 40$), respectively.

Dispersal

Queen dispersal is not only important for colonizing empty habitats, but also for lowering the extinction chance of local conspecific populations by means of adoption. Dispersal by means of worker transport (nest budding) is only possible for nest populations which have more than one queen. Dispersal by means of walking could be rewarding for young queens in areas where flying is very risky, *e.g.* in an archipelago (ROSENGREN & PAMILO, 1983) or in areas where the nest density of the host species (*i.c.* *F. fusca*) is very low (KUTTER, 1964). However, transport distances are very small in our study area and daughter nests are generally built at a distance of less than a few metres from the mother nest. Dispersal over longer distances is only possible by means of young queens, which can fly.

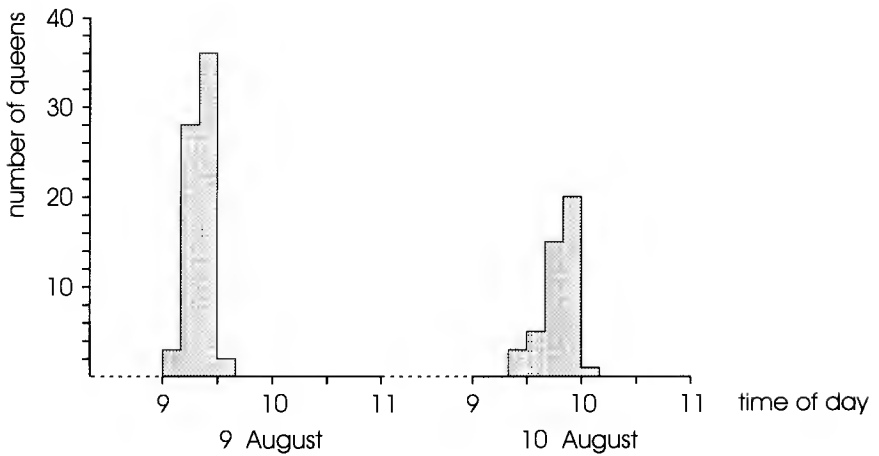


Fig. 8. Number of *F. truncorum* queens leaving a nest on two successive days: 09-10/08/1995.

Males and queens started flying in the early morning on a warm, nearly windless day. About one third of the queens that left the nest flying landed within a distance of 20 m from the nest. Most of them climbed into grass stems, bushes or trees from which they started their next flight. How far they will fly is difficult to investigate. If dispersal distance is important for colonizing vacant habitat patches, we may expect that the queens will profit from some wind by starting their flight against the wind to gain height and then fly with the wind to get farther away. In fact there is no correlation between wind and flight direction. A wood ant queen is able to fly several kilometres (MABELIS, 1994), but then she will leave the habitat patch. A virgin queen who does so has a lower chance of meeting a male and of finding a suitable nesting site. The distribution pattern of occupied habitat patches gives an indication that most queens (ca. 80%) will not fly farther than two kilometres.

Orientation

For establishing a colony a queen has to be fecundated. The meeting chance between queens and males could be enhanced if both sexes fly to a common area on the ground near the nest, as observed in *F. obscuripes* (TALBOT, 1959, 1972), or if both sexes orientate towards a common area farther away, as reported for several *Formica* species in mountainous areas of Canada and the United States (CHAPMAN, 1954, 1957, 1969), but no aggregations of the sexes were observed around objects, which were prominent on the horizon, like a lookout tower or trees.

In order to find out how queens orientate during their flight, we observed the flight behaviour of queens from nests with a different position with respect to the forest edge. It appeared that they did not orientate to the sun and that they did not profit from the wind (if there was any). Figure 9 shows that they flew in the direction of open areas and that they avoided woodland. Red wood ant queens are probably able to orientate on the pattern of the landscape. Males may also have this ability, as no differences between the sexes in flight orientation were noted. Their meeting chance will be highest in the core area with the highest nest density.

Establishment

A wood ant queen is not able to care for her own brood: she is dependent on workers who have to perform this task (GÖSSWALD, 1952, 1989). For reproduction a queen should be adopted by a nest population of her own species or another species (*i.e.* *F. fusca*). For the establishment of a new colony adoption by *F. fusca* is necessary. The chance that this will happen is very low. In a period of seven years, four mixed nests *F. truncorum* — *F. fusca* were observed. It seems as if *F. truncorum*-queens are more easily adopted by *F. fusca* than the other red wood ant species, as mixed nests *F. rufa* — *F. fusca* and *F. polycтена* — *F. fusca*, are very seldom observed. However, a mixed nest is no proof of successful colonization, as robbing pupae from a *F. fusca* nest by *F. truncorum* workers is possible, as we observed once. The higher the nest density of the host species *F. fusca* in a habitat patch, the greater the chance that the patch will become (re)colonized by *F. truncorum*. The discovery of a new nest, as shown in table 1 (nest numbers: 12, 13, 19, 25), is not always the result of the establishment of a new colony: it may be due to nest splitting (budding) or to the removal of a nest population to a new nest site. If such processes took place in spring or autumn, *i.e.* outside the observation period, we can just guess if it was a colonization or not. So it may be that the number of colonizations are overestimated. On the other hand new nests can be easily overlooked. Therefore a group of volunteers was asked (in 1990) to survey the core area systematically. However, only one new nest (nr. 25) was discovered.

DISCUSSION

Nest populations of *F. truncorum* may be more prone to extinction than those of *F. polycтена* and *F. rufa* for the following reasons:

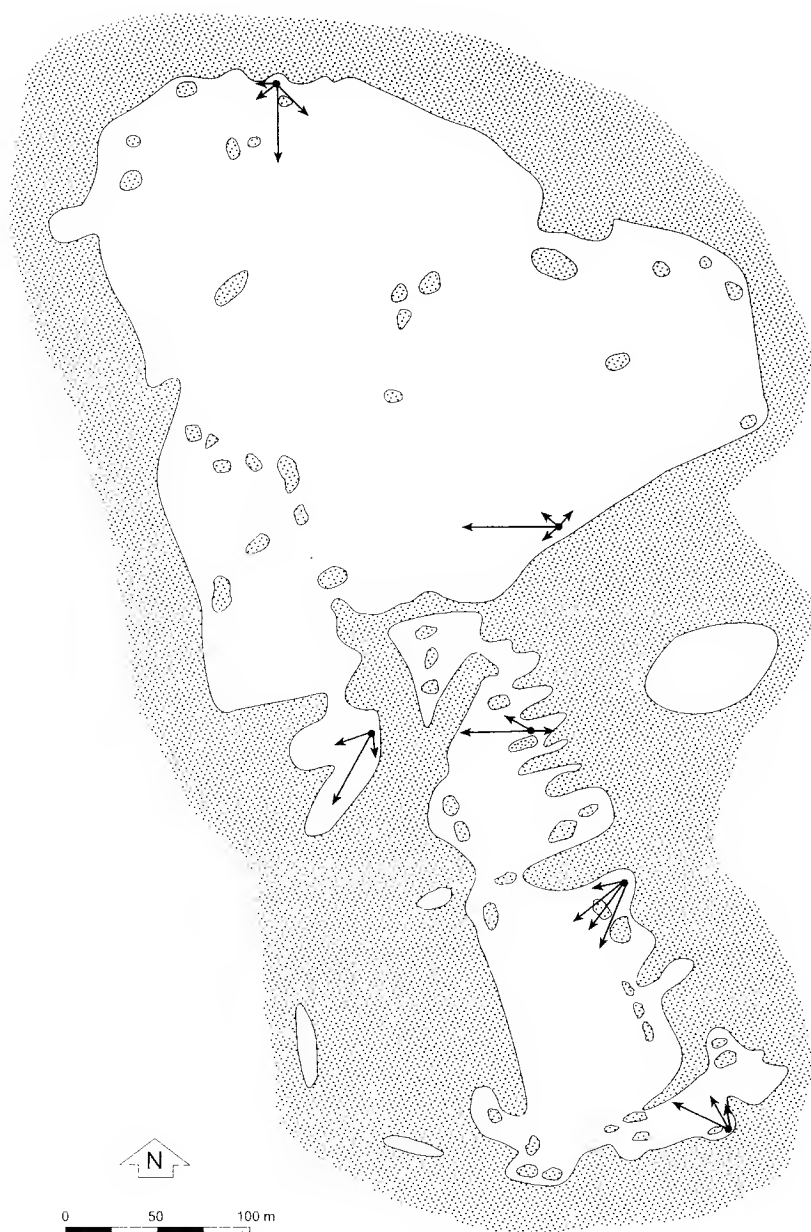


Fig. 9. Orientation of queens flying from nests with a different position with respect to the surrounding woodland; arrows indicate the percentage of queens flying in that direction (data from summer 1990 + 1995; number of observations: ca. 100 per nest).

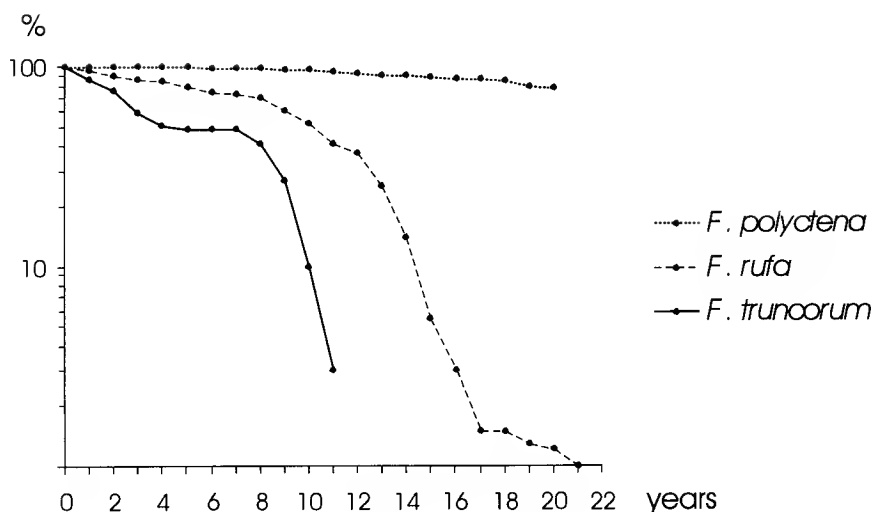


Fig. 10. Extinction rate of three species of red wood ants, which differ in the number of queens in their nest. Nest survey *F. polystena* and *F. rufa* in NP. De Hoge Veluwe (data from E.T.G. Elton), nest survey *F. truncorum* in Boswachterij Ommen.

1) *F. truncorum* nests are relatively small and messily built. The inability to maintain thermal homeostasis implies a greater dependency on external heat for raising its brood than the other red wood ant species (KATÔ, 1939; ROSENGREN *et al.*, 1985). Consequently, a nest population has to move as soon as the nest gets too much shade as a result of tree growth.

2) Nest sites of *F. truncorum* will not persist for a long time, at least not in the sandy areas of west and middle Europe: they deteriorate more quickly than nests of *F. rufa* and *F. polystena*. So nest populations have to move more often. This will be especially the case in situations where the density of proper nest sites, like tree trunks, is low and the ants have to build their nest against grass tussocks. *F. truncorum* may be better off on the rocky islands of the Finnish archipelago, where the trunk ants build their nests mainly around large stones and in rock crevices, *i.e.* a stable habitat, which can keep heat for a long time (BRANDT, 1980). However, naked rock will set a limit to the growth of nest units for physical, as well as for nutritional reasons, as the food situation may be rather poor in this type of habitat (ROSENGREN *et al.*, 1985). ROSENGREN *et al.* (1985) observed that foragers walk 40 m from their nest, while the maximum foraging distance in our study area is about 20 m. Increasing foraging distance will favour decentralized nesting in polygynous colonies (HÖLLDOBLER & LUMSDEN, 1980; CHERIX,

1980), which may explain the development of polydomous colonies on the Finnish islands (ROSENGREN *et al.*, 1985). Exchange of workers between nests and seasonal movements of nest populations between winter- and summer nests are observed regularly (ROSENGREN & PAMILO, 1983; ROSENGREN *et al.*, 1985). The social mobility between nest sites is high: the ants can adapt quickly to the environment, choosing optimal sites for overwintering and reproduction. The result is that only 40% of the nests stayed inhabited throughout the year. This contrasts sharply with the situation in sandy areas of the Netherlands, Germany and Poland: *e.g.*, in our study area ca. 85% of the nests are single and the majority of these nests (70-80%) stayed inhabited throughout the year. Locally nestpopulations moved more often, due to recreation pressure or to measures of management, as on the Besthmenerberg in 1995. However, under these circumstances more than 60% of the nests stayed inhabited. The foraging areas of nest populations were rather fixed and did not overlap, as we observed by laying prey in the border area between nests (fig. 4).

3) *F. truncorum* colonies in our study area are largely monodomous. This makes them more vulnerable than polydomous colonies, as their risk of extinction is not spread in space (ROSENGREN & PAMILO, 1983; MABELIS, 1986; ROSENGREN *et al.*, 1993). In situations where nest material can be spread along the edge of a fallen tree or along stone crevices (as in Finland), the workers of a polygynous colony will be stimulated to build small nest mounds in suitable places and connect them with narrow strips of nest material. The queens will be distributed among the nestmounds which belong to the same "supernest" (ROSENGREN *et al.*, 1985). Such an extended nest system will favour young queens to stay instead of flying away, as competition between them can be largely avoided. Consequently, more *F. truncorum* colonies will be polygynous in the Finnish Archipelago than in our study area. As those nests are situated on islands, polygyny may have evolved to avoid the risk of young queens leaving the island in search of another habitat patch (ROSENGREN & PAMILO, 1983). By staying in the mothernest daughter queens can avoid dispersal risks, but then the mother queen has to compete with her daughters, unless this can be avoided by nest budding. However, for the forming of a polydomous colony, the habitat should be sufficiently large and stable. In a situation where small habitat patches are scattered over the distribution area, selection may favour monogyny and dispersion will occur by means of flying daughter queens (ROSENGREN & PAMILO, 1983; MABELIS, 1986, 1994; HEINZE, 1993). So polygyny will not always be favoured in patchily distributed habitats, as HÖLLDOBLER & WILSON (1977) suggested. The assumption that a great deal of the nests

in our study area are monogynous is supported by the fact that a majority of the nests stayed single during a period of at least seven years and by an observation of Zaaijer (pers. comm.): in an artificial nest he observed that two groups of 300 workers did not accept more than one winged queen of their own colony; the other queens were killed (*i.e.* 9 in both cases). Workers from some other nest populations were accepted, but not their queens.

4) Nest populations of *F. truncorum* have only one queen or a few queens, while nests of *F. rufa* generally contain more queens and nests of *F. polystena* much more queens. *F. truncorum* will hold less queens in reserve and has a smaller worker force. Consequently, it is a weaker competitor and its territory is much smaller than that of the other species (*i.e.* 55-750 m², 213 m² on average). On the basis of the data mentioned above, we expect that the extinction rate of *F. truncorum* colonies will be much greater than that of *F. polystena* and also greater than that of *F. rufa*. Figure 9 indicates that this may be the case, although the data of *F. rufa* and *F. polystena* are collected in another year and in another area (MABELIS, 1986). The expectation that the extinction rate of *F. truncorum* colonies will be greater than that of the other red wood ant species is supported by the fact that the extinction rates of the three species followed a similar trend in our study area.

In order to survive, the greater extinction chance of *F. truncorum* should be compensated by a greater colonization chance (table 2). The colonization chance of a habitat patch depends on the number of queens produced by the nearest nests, the chance that they will become fertilized, their ability to disperse, orientate and their chance to become adopted by a host species. It appeared that nest populations of *F. truncorum* produced less sexuals than those of the other red wood ant species. However, more *F. truncorum* nests produced sexuals yearly than *F. rufa* and *F. polystena* nests. The fact that the number of nests of a polygynous population produced less sexuals is in accordance with findings in another area (Sallandse Heuvelrug). Nests of monodomous red wood ant colonies produced relatively more sexuals in a year than nests of polydomous colonies (χ^2 test: $0.01 < p < 0.025$). Accordingly, the proportion of monodomous *F. truncorum* colonies producing sexuals in the Finnish Archipelago was higher than that of polydomous *F. truncorum* colonies: 65% and 19-52% of the colonies, respectively (ROSENGREN *et al.*, 1986). So it is not surprising that the proportion of *F. truncorum* colonies producing sexuals is greater in our study area (70-85% per year) than in the Finnish Archipelago, where the nests are largely polydomous (25-40% per year; see ROSENGREN *et al.*, 1993). The colonization chance of habitat patches in our study area is also enhanced by the fact that

TABLE 2

Difference in extinction and colonization probability of three species of red wood ants.

Species	Queen number			Size nestpopulation	<i>p</i> extinction	<i>p</i> colonization
	one	few	many			
<i>F. polystena</i>			+++	very large	very small	very small
<i>F. rufa</i>	++	++	(+)	large	small	small
<i>F. truncorum</i>	++	++		small	large	?

both sexes are more prone to disperse in a monogynous colony than in a polygynous one (SUNDSTRÖM, 1995).

To establish a colony a queen has to be fecundated. In nests where both sexes are present at the same time, it will be possible to mate in the nest or on the surface of the nest, as observed by ROSENGREN *et al.* (1986). Intranidal mating is supported by the finding that the genetic relatedness between workers and queens in polygynous colonies is high (SUNDSTRÖM, 1993). In our study area we did not see copulating *F. truncorum* queens on or near the nest. Males took flight immediately after they appeared on the nest surface. It may be that these monodomous nests had only one queen, as males from monogynous nests prefer to fly instead of mating (ROSENGREN *et al.*, 1993; SUNDSTRÖM, 1995). The chance of a male meeting a queen may be enhanced by the short daily flying period of both sexes, *i.e.* between 08-11.00 h, while sexes of the other red wood ant species can fly between 09-16.00 h. Moreover SUNDSTRÖM (1995) found that queens from monogynous colonies generally have a longer searching time to find males from other colonies and a suitable nesting place, as they lose their wings later than queens from polygynous colonies. Both sexes flew on warm, nearly windless days, as observed by CHAPMAN (1954, 1957) and TALBOT (1959). If there was any wind, they did not fly downwards, as observed on Finnish islands (ROSENGREN *et al.*, 1986), nor did they orientate to the sun, as suggested by the same authors. In fact they flew in the direction of open areas and avoided woodland, increasing the chance of finding a nest population which will adopt them. The impression that queens are able to orientate on the pattern of the landscape is supported by the observation of some *F. truncorum* queens that oriented on an island silhouette while flying over the sea (ROSENGREN *et al.*, 1986) and by the observation of swarm locations of *F. subnuda* queens, in which vision plays an important role (CHAPMAN, 1969). It may be that sexuals will fly in all directions in open landscapes without trees, as observed in *F. obscuripes* (TALBOT 1959), or that they will fly downwind as observed in *F. truncorum* on a treeless skerry of an island (ROSENGREN *et al.*, 1986).

The reproductive success of a red wood ant queen depends upon her ability to orientate on microhabitats where the chance of becoming adopted by a nestpopulation is highest. To colonize a vacant habitat patch a queen should be adopted by a nest population of *F. fusca*. To compensate the great extinction chance of nest populations the adoption chance of queens should be great: greater than for *F. rufa* and *F. polycтена*. A *F. rufa* queen has a greater chance of becoming adopted by *F. fusca* than a *F. polycтена* queen, according to adoption experiments by GÖSSWALD (1952). Data about the adoption chance of *F. truncorum* queens are lacking. *F. truncorum* appears to be more opportunistic than *F. rufa* and *F. polycтена*; its queens are able to colonize small and temporary habitat patches, where their nest populations can live for a relative short period of time: ca. 8 years in our study area. Our observations are in agreement with those of SEIFERT (1996; pers. comm.). *F. truncorum* seems to be adapted to such a patchy environment with short-lived nest sites. However, there are no arguments to assume that *F. truncorum* is less vulnerable than *F. rufa* or *F. polycтена*. On the contrary, its survival chance seems to be less. It is worthwhile to find out if *F. truncorum* is an endangered species.

ACKNOWLEDGEMENTS

We thank Dr. E. Tobach and Drs. G.J. de Bruyn for their valuable comment. We are also thankful to Mrs. J. Whittaker for improving the english text.

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